

Composition and resources of photosynthetic pigments of the sea phytoplankton

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BOGDAN WOŹNIAK, MIROSLAWA OSTROWSKA

Institute of Oceanology,
Polish Academy of Sciences,
Sopot

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Abstract

The paper contains a review of own and based on literature data concerning the time-space changes of sea phytoplankton resources in different areas of the World Ocean. Sets of photosynthetic pigments that occur for various groups of sea phytoplankton are also quantitatively characterized. Moreover, the results of statistical analysis of the pigment composition of natural populations of phytoplankton (so-called phytocenoses) are also presented. These analyses were made for both various biological types of seas and oceans and various depths in the sea.

1. Introduction

This article is a third work in a row concerning the optical (absorption and fluorescence) properties of sea phytoplankton and fluorescence methods of photosynthesis investigations. In the previous works the luminescence phenomena and the accompanying phenomena in sea water were analyzed (Ostrowska and Woźniak, in press). Phytoplankton photosynthetic pigments and their individual optical properties were also discussed (Woźniak and Ostrowska, in press).

Apart from the individual, optical properties of the pigments, two other factors determine the total and absolute (absorption and fluorescence) properties of water samples containing phytoplankton. They are: phytoplankton concentration and characteristic for it pigment sets. These

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factors are analyzed in this article. Main goals of this work are: characterization of the time-space changes of sea phytoplankton resources for different areas of the World Ocean and determination of the typical photosynthetic pigment sets of phytoplankton.

These goals are achieved on the basis of our own results and the results available in the literature. Moreover, the results of the statistical analysis of pigments of phytoplankton natural populations (so-called photoceneses) are presented. These analyses are made with respect to various both biological types of seas and oceans and various depths in the sea.

As the biological type of a sea or the ocean we understand in this paper the class of its biological productivity. As a measure of the basin productivity the most often accepted (see: *Biologiya okeana* – group work under Vinogradov, 1977) is the chlorophyll *a* $Ba(0)$ surface concentration. This parameter indicates the potential production possibilities of water and correlates with the total (*i.e.* in water column) primary production of a basin (Kobelentz-Mishke and Vedernikov, 1977; Woźniak, in prepared). We accepted four biological types of basins according to the following scheme (Tabl. 1):

Table 1: Waters division into biological productivity classes

Biological type of basin and symbol used in this paper	Productivity class	Range of surface chlorophyll <i>a</i> concentration changes $Ba(0)$ [mg/m^3]
Oligotrophic basins O	small productivity	< 0.2
Mesotrophic basins M	mean productivity	$0.2 \div 0.5$
Transient basins meso-eutrophic P	transient mean (high productivity)	$0.5 \div 1.0$
Eutrophic basins E	high productivity	> 1

Often in this paper the name of the biological type of a basin is related to phytocenosis, *e.g.* oligotrophic phytocenosis one should understand as the phytocenosis of an oligotrophic basin, *i.e.* phytoplankton natural population in an oligotrophic sea.

2. Location and seasonal changes of the phytoplankton resources in the World Ocean

2.1. Main natural conditions of phytoplankton resources in the World Ocean

The most important factors that conditions the sea phytoplankton resources are among others: irradiance conditions and biogen concentration in a sea, temperature, and density stratification of water masses that result from their thermal and dynamical states (Steeman Nielsen, 1975; Bougies, 1976). The variety of the above factors that one can face in nature influences the time-space variety of natural resources of phytoplankton in different areas of the World Ocean.

The most productive, hence the most abundant as for as phytoplankton is concerned, are the areas where under "good" irradiance conditions also sufficiently high contents of biogens occur.

In ocean the photosynthetic layer is supplied with biogenes mainly by waters upwelling from depths and carrying biogens from the bottom. These processes may occur because of the vertical convection of water masses and upwelling caused by the winds from land (Druet and Kowalik, 1970), current divergences, cyclone centres and also underwater peaks (Mordasova, 1976). Occurrence of the above factors positively influences the fertility of the photosynthetic layer, their lack causes the existence of non-productive areas.

The influence of stratification on primary production is not explicit and shows differentiation depending on the climatic zone and the season.

For example in temperate and cold basins, in which seasonal temperature variations occur, both the appearance and disappearance of the stratification influences always positively the phytoplankton growth (Semina, 1957). During summer, under intense heating, a strong stratification appears, which partly prevents both living and dead plankton cells from gravitational falling from the euphotic zone. Due to this the living plankton, as well as biogens which are the products of the decay of dead cells remain in the photosynthetic zone. Thus the stratification causes phytoplankton growth intensification, which results in high pigments concentrations. Winter cooling reduces stratification, but on the other hand it helps creating currents carrying biogens from deeper layers. Opposite situation takes place in tropical areas of the World Ocean. In these areas,

where basically seasonal temperature changes do not occur, water masses stratification is relatively constant. It prevents creating currents carrying the biogens from deeper layers.

That is why the tropical areas of the oceans, although "well" irradiated, are mostly the least productive areas of the World Ocean.

The above presented conditions of sea productivity relate mainly to open oceanic areas. Most often they do not relate to semi-open oceanic areas (gulfs) and inner seas (*e.g.* Baltic, Black Sea). In these basins the most important influence on phytoplankton growth and concentration usually have local factors, which show strong differentiation. Therefore it is impossible to present an explicit description of the mechanism that condition their productivity. Generally, however, these seas are very productive basins. This is due to a strong supply in biogens by the inflowing river waters. Often a positive role, mainly in the case of shallow seas, is played by strong mixing of surface and bottom waters.

The conditions of primary production of phytoplankton and its pigments concentration in water, discussed qualitatively in this paper, are confirmed by the chlorophyll *a* distributions in the World Ocean presented in the further part of this chapter.

2.2. Chlorophyll *a* distribution in the World Ocean

As an indicator of phytoplankton resources in a sea the main photosynthetic pigment, *i.e.* chlorophyll *a*, is most often used. From the literature data on the content of this pigment in various areas of the World Ocean, majority relate to its concentration in surface layers of the seas, or to the total content in water column under a unit surface. On the basis of these data various authors (*e.g.* Mordasova, 1974a, b; Krey, 1971, 1973; Krey and Babenerd, 1976) prepared maps of chlorophyll distribution for chosen seasons and different oceans (separate for Atlantic, Pacific and Indian Ocean). The summary, however, for the whole World Ocean area was made by Mordasova (1976). The results were based on statistical analysis of data from about 5.500 stations located in different areas of the World Ocean. Since the seasonal changes in chlorophyll content in tropical and subtropical areas from 40°N to 40°S are minimal (besides few exceptions), while preparing the maps for these areas all the experimental data, independently of the time of observation, were used. On the other hand, north and south of this zone the chlorophyll concentrations

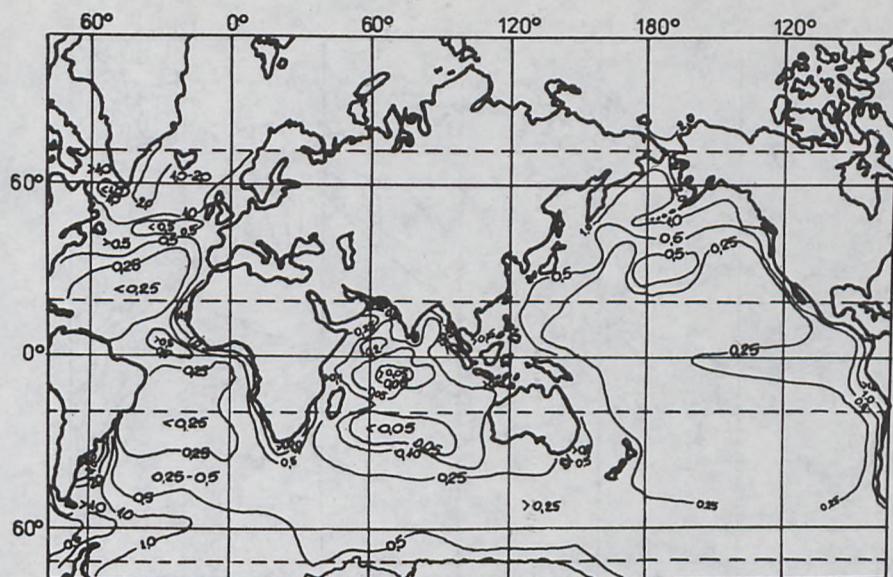


Figure 1: Chlorophyll *a* concentration distributions in surface layer of the World Ocean $Ba(0)$ [mg/m^3] (Mordasova, 1976)

measured in spring–summer season, *i.e.* the vegetations season, were taken into account.

The results obtained by Mordasova are shown in Figures 1 and 2. The presented maps illustrate the chlorophyll *a* concentration distributions at the sea surface $Ba(0)$ [mg/m^3] (Fig. 1), and the distributions of the integral content of this pigment in water column, from the surface to a depth of 100 m, under a unit surface $\Sigma_{0m}^{100m} Ba(z)$ [mg/m^2] (Fig. 2)². The specificity of the above distributions and their regional character are analyzed in details in Mordasova work (1976). Here we limited ourselves to the most important regularities.

- On the open oceanic spaces, waters rich in chlorophyll, *e.g.* with $Ba(0) > 1 mg/m^3$ (*i.e.* transient waters between meso- and eutrophic, as well as eutrophic basins), occur rather seldom and on small areas. In low and temperate geographic zones such basins are known only in continental shelf areas. These areas are richer in biogens owing to river confluence, or – for western continental coasts

²We stress that the second of these distributions, because of the modest statistics, is less exact than the first one.

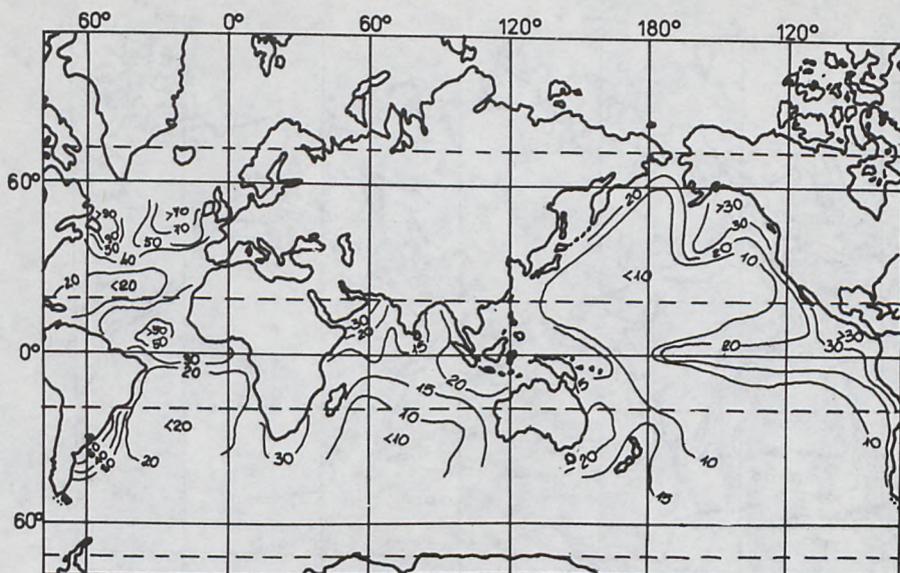


Figure 2: Total chlorophyll *a* content distribution (in 0 to 100 m layer) in the World Ocean $\sum_{0m}^{100m} Ba(z)[mg/m^2]$ (Mordasova, 1976)

- owing to upwelling, carrying the biogens from deeper layers. Basins with $Ba > 1 mg/m^3$ occur more often in cold oceanic areas ($\varphi \sim 50^\circ \div 70^\circ$), especially in antarctic and arctic circulation areas.
- Oceanic areas in temperate northern zones are characterized by slightly smaller amounts of chlorophyll *a*, $Ba(0) \sim 0.5 \div 1 mg/m^3$, hence characteristic for transient meso- and eutrophic waters.
- Relatively small areas around the Equator are most often mezotrophic basins with concentration $Ba(0)$ close to $0.25 mg/m^3$.
- The most extensive parts of the oceans, are the oligotrophic waters, leanest in phytoplankton. They occur in tropical and subtropical parts of the ocean and in the zones of waters leave in the northern and southern anticyclonic vortexes. In these areas the chlorophyll *a* concentration decreases to $Ba(0) < 0.25 mg/m^3$ in Atlantic and Pacific, and for Indian Ocean it can be even lower, $Ba(0) < 0.05 mg/m^3$.

The above discussed regularities basically relate to open ocean areas. Distributions shown in Figures 1 and 2 do not regard the chlorophyll *a*

concentrations characteristic for closed waters. In the world literature there are a lot of works that deal with the analysis of pigments' concentration distributions in these basins³. It appears that phytoplankton concentrations in closed seas usually reveal significant time and spatial changes. Therefore it is impossible to explicitly determine the pigments concentration characteristic for a particular sea. Generally, however, they are basins, usually more abundant in phytoplankton than oceans. Most often they can be classified as transient between meso- and eutrophic (*e.g.* central part of the Middle Baltic with $Ba(0)$ in a range $0.5 \div 1.2 \text{ mg/m}^3$ - authors' data, and also about a half of the Black Sea area with $Ba(0)$ in a range $0.5 \div 0.8 \text{ mg/m}^3$ - authors' data). In coastal areas they are usually eutrophic basins with concentrations reaching in extremal cases a dozen or even a few tens mg/m^3 of chlorophyll *a* (Malewicz *et al.*, 1974). Even higher concentrations are sometimes encountered⁴. More seldom closed seas are characterized by $Ba(0)$ concentrations typical for mesotrophic basins (*e.g.* central part of the Black Sea with $Ba(0) \sim 0.2 \div 0.6 \text{ mg/m}^3$ - authors and co-workers data, Koblentz-Mishke *et al.*, 1985a, b), or even more clear (*e.g.* open waters of Mediterranean Sea with $Ba(0) \sim 0.1 \div 0.5 \text{ mg/m}^3$ - according to Herrera and Margalef, 1961).

2.3. Seasonal changes of phytoplankton resources in the basins and their correlation with latitude

Seasonal variations of chlorophyll *a* concentration in the World Ocean are not sufficiently investigated. In the world literature one can find only some data concerning this subject and related to chosen oceans and seas⁵.

Examples of such seasonal changes in various seas are illustrated in Figure 3. It is impossible, however to generalize this problem, which would allow the quantitative estimations of seasonal chlorophyll *a* variations in different areas of the World Ocean and at various depths.

Some qualitative idea of these changes is given in the Bogorov's work (1974). Basing on other works he characterized mainly the tendencies of

³*e.g.* Renk, 1973; Torbicki, 1975; Malewicz *et al.*, 1974 - in Baltic; Sorokin, 1982; Vedernikov *et al.*, 1980 - Black Sea; Steeman Nielsen *et al.*, 1969; Herrera and Margalef, 1961 - Mediterranean Sea.

⁴*e.g.* during the International Experiment SOZOPOL - 1986 during the spring-summer season in the Gulf of Burgas area (Black Sea) the chlorophyll *a* concentration reached 0.5 and even more kg/m^3 (unpublished data of the international research group including the authors)

⁵Atkins and Jenkins, 1953; Herrera and Margalef, 1961; El-Sayed, 1968, 1970; Deharai and Bhargava, 1972; Chan, 1973; Renk, 1973; Malewicz *et al.*, 1974; Renk *et al.*, 1978; Fransz, 1985; Therriault and Levasseur, 1985.

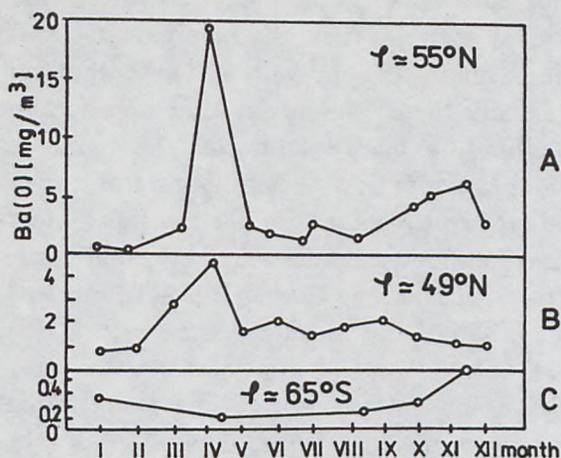


Figure 3: Exemplary seasonal changes of chlorophyll *a* concentration $Ba(0)$ in surface waters: A - Southern Baltic (Rønk, 1973); B - North Sea (Fransz, 1985); C - Southern Pacific (El-Sayed, 1970)

seasonal changes of sea phytoplankton for different climatic zones. This is illustrated in Figure 4, in which the independent variables (*i.e.* phytoplankton amount) are expressed only approximately in uncomparable and uncalibrated units.

Because of the representativity of chlorophyll *a* as the phytoplankton biomass indicator, we can accept that Figure 4 illustrates also qualitatively the chlorophyll *a* concentration changes during a year.

As one can see from the above Figure, in temperate zones two phytoplankton blooms (*i.e.* increase of chlorophyll concentration) are observed, in fall (August, September) and in spring (March). Usually the spring maximum is higher than the fall one. The time interval between these blooms is half a year. Going to higher latitudes, delaying of the spring bloom is observed and acceleration of the fall one. As a consequence, in Polar Zone these maximums completely overlap and only one bloom is observed during the polar summer, in June. These regularities are a natural consequence of astronomic factors (Earth axis slope and its orbiting around the Sun) that condition the 24 hours cycles and the seasons.

On the other hand, with a decreasing latitude from the temperate zone to the Equator, opposite tendencies are observed, *i.e.* earlier spring blooms and later fall blooms. As a result, in the tropical zone these two concentration maximums also overlap, so that one bloom is observed

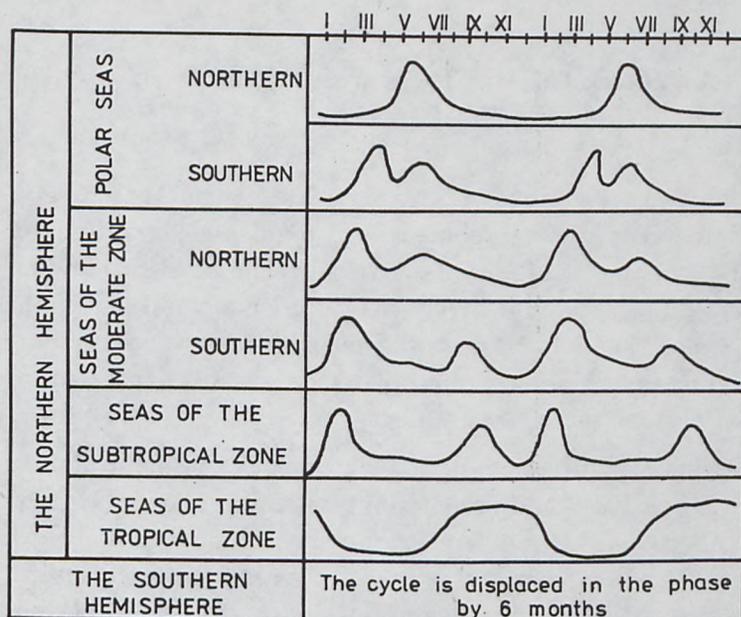


Figure 4: Illustration of seasonal changes of the phytoplankton content for different climatic zones of the World Ocean (Bogorov, 1974).

during winter. The apparent paradox of higher plankton amount in winter compared to summer can be elucidated by changes in activity of the entire ecosystem, manifesting themselves through *e.g.* higher rate of phytoplankton grazing by zooplankton in summer compared to winter, and by depletion of the biogens supply.

Moreover – which is not visible from Figure 4 – the amplitudes of the observed seasonal changes of the phytoplankton amount are strongly differentiated depending on the latitude (Mordasova, 1976). On Equator and in the tropical zone they are small, yet they strongly increase with an increase in the latitude. This is mainly due to annual sea temperature and irradiance (sunlight) cycles. These quantities are rather constant on Equator and strongly differentiated for higher latitudes (*e.g.* Dera, 1983).

3. Composition of phytoplankton photosynthetic pigments in the World Ocean

3.1. Pigment sets characteristic for various groups of phytoplankton

Composition of pigments for various photosynthetic organisms is strongly differentiated. There exist, however, some sets of pigments characteristic for the particular components of the plant world. The sets for various sea phytoplankton groups are qualitatively characterized by data given in Table 2 (Parsons *et al.*, 1977). It presents the occurrence of the particular photosynthetic pigments in main sea phytoplankton groups, expressed in three-degree scale: always, often, sometimes.

As one can see, chlorophyll *a* occurs in all groups as the main photosynthetic pigment. Besides, for different phytoplankton groups various completing pigments sets are found. For example, chlorophyll *a* is always accompanied by carotenoids from both groups of carotenes and xanthophylls. This is due to the protective role (against photooxidation) played by these pigments in a cell. The occurrence of other completing pigments, *i.e.* chlorophyll *b* and *c* and phycobilins, depends on the group. One can distinguish three different phytoplankton types, and also vascular plants (Parsons *et al.*, 1977). In these types, apart from protective carotenoids and chlorophyll *a*, also the following pigments occur as the light energy antennas: type I - chlorophyll *c* and carotenoids that assist absorption, type II - chlorophyll *b*, type III - phycobilins.

The first of these types is the most frequent among natural phytoplankton populations. Type II is characteristic rather for vascular plants. In sea phytoplankton, chlorophyll *b* is found only for one group (Parsinophyceae). Even more seldom is type III, because the two groups in which phycobilins occur (Myxophyceae and Cryptophyceae) are very seldom in natural phytocenosis.

Table 2: The occurrence of pigments in different classes of marine phytoplankton (after: Parsons *et al.*, 1977)

Pigments	Bacillario-Myxo-Chloro-Myxo-Xantho-Crypto-Prasino-Hapto-phyceae phyceae phyceae phyceae phyceae phyceae phyceae								
	Bacillario-phyceae	Dino-phyceae	Chryso-phyceae	Chloro-phyceae	Myxo-phyceae	Xantho-phyceae	Crypto-phyceae	Prasino-phyceae	Hapto-phyceae
CHLOROPHYLLS									
<i>a</i>	***	***	***	***	***	***	***	***	***
<i>b</i>				**				**	
<i>c</i>	**	**	*			(*)	**		**
CAROTENES									
α	***	***	***	***	***	***	***	*	
β	***	***	***	***	***	***	***	***	***
γ								*	
XANTHOPHYLLS									
fucoxanthin	***	(*)	***			***		***	***
neofucoxanthin	**		**						**
diadinoxanthin	**	**	**			**		**	**
diatoxanthin	*					*			*
peridinin		***							
dinoxanthin		*							
neoperidinin		*							
lutein				***				**	**
zeoxanthin				*				*	
flavoxanthin				*					
violaxanthin			*	*				**	
neoxanthin				*					
alloxanthin				*				**	**
monodoxanthin							*		
crocoxanthin							**		
myxoxanthin					**				
myxoxanthophyll					**				
anthraxanthin					(*)				
siphonaxanthin				*					
PHYCOBILINS									
number of unidentified pigments		2		1		1		2	8
Description of pigments occurrence: *** - always, ** - often, * - sometimes, () - presence uncertain									

3.2. Pigments composition in various natural phytocenoses

The results presented in the previous paragraph characterize only qualitatively the pigment sets of various phytoplankton groups. That is why they can not be utilized for quantitative estimations of the optical properties of natural phytoplankton populations in the sea, the more that natural phytocenoses of natural phytoplankton representatives of different groups and species. An introductory quantitative description of the composition and concentration of pigments in photosynthetic apparatus of various natural phytoplankton populations was elaborated by Woźniak (in prepared). The description is based on statistical analysis of the experimental data from about 1000 stations located in different regions of the World Ocean. Concentrations of the particular photosynthetic pigments *i.e.* Ba - chlorophyll *a*, Bb - chlorophyll *b*, Bc - chlorophyll *c*, $\sum Bk$ - total carotenoids concentration, as well as the colour index C_{In} (see next paragraph) were analyzed. These quantities were analyzed with respect to both various biological sea and ocean types, and to various depths in the sea. Some more important results are presented in this paragraph and in the two following ones.

In Figure 5 the statistical courses (mean and standard deviations) of the relative contributions of the content of the particular phytoplankton pigments in the total pigment concentration, depending on the chlorophyll concentration Ba , are shown. The relative contributions are described as the following ratios:

$$\epsilon_a = \frac{Ba}{\sum B}; \quad \epsilon_b = \frac{Bb}{\sum B}; \quad \epsilon_c = \frac{Bc}{\sum B}; \quad \epsilon_k = \frac{\sum Bk}{\sum B}, \quad (1)$$

where:

$$\sum B = Ba + Bb + Bc + \sum Bk, \quad (2)$$

is the total content of all the pigments in unit sea water volume, except the phycobilins.

The above mentioned relative contributions are related in Figure 5 to chlorophyll *a* concentration as the indicator of the biological type of a basin. Similar relations as in Figure 5, but concerning the absolute concentrations of the particular pigments, are presented in Figure 6. As one can see from these Figures, neglecting the scatter of the experimental data, one can notice significant tendencies for pigments composition changes depending on the biological type of a basin. Changing from biologically

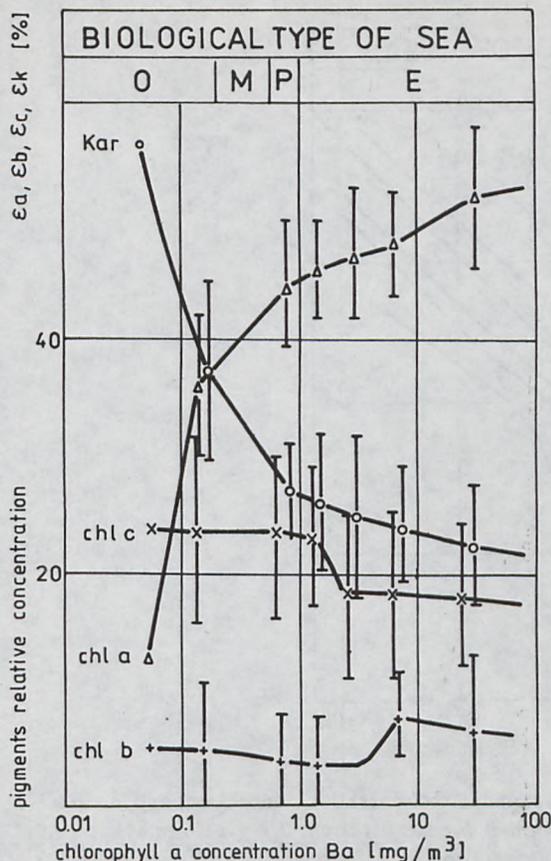


Figure 5: Statistical courses of the relative content contributions of the particular phytoplankton pigments, in the total pigments concentration, depending on chlorophyll *a* concentration. Vertical segments relate to standard deviations of the observed magnitudes of these contributions (Woźniak, in prepared)

rich, eutrophic waters to lean oligotrophic basins, the relative share of pigments accompanying chlorophyll *a* increases. For highly productive eutrophic basins, the chlorophyll *a* concentration reaches almost 60% of the content all the pigments, while the total contents of all the other pigments is a little more than 40%. On the other hand, in biologically lean basins the situation changes – in the case of the cleanest, oligotrophic basins the chlorophyll *a* concentration decreases to almost 10%, while the accompanying pigments dominate. Their total concentration reaches 90%.

From among the three analyzed groups of accompanying pigments (chlorophyll *b*, chlorophyll *c*, carotenoids) the smallest concentrations

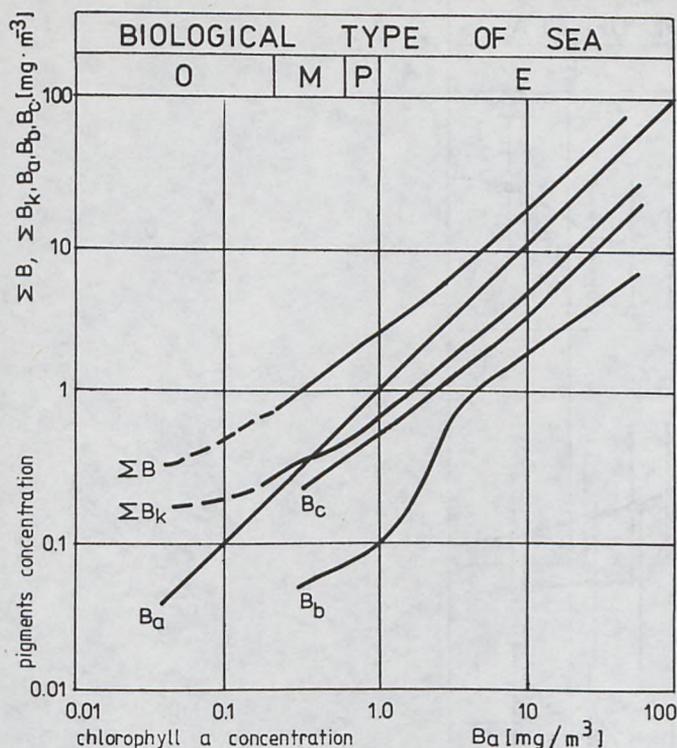


Figure 6: Dependences of the absolute pigment concentrations on chlorophyll *a*. B_a - chlorophyll *a* concentration, B_b - chlorophyll *b* concentration, B_c - chlorophyll *c* concentration, ΣB_k - total carotenoids concentration, ΣB - total concentration of all the pigments except phycobilins (Woźniak, in prepared)

characterize chlorophyll *b*, whose contribution to the total pigment mass is most often significantly smaller than 10%. The accompanying pigments are chlorophyll *c* and mainly carotenoids. Concentration of the latter in oligotrophic seas is on average two times higher than the chlorophyll *a* content, and in extreme cases can be even 4 times higher. This is illustrated in Figure 7, presenting the changes in the concentration ratios for various biological basin types. As one can see from this Figure, in eutrophic seas, *i.e.* under conditions favouring photosynthesis, an optimum pigment set is settled (about 55% of chlorophyll *a* and ca 45% of accompanying pigments). If, however, the vegetative conditions for phytoplankton are worse (*e.g.* in lean oligotrophic basins), the organisms initiate the defensive processes. According to many authors (*e.g.* Margalef, 1967; Koblentz-Mishke, 1971) adaptation processes to "worse" conditions reveal through an increase in additional accompanying pigments

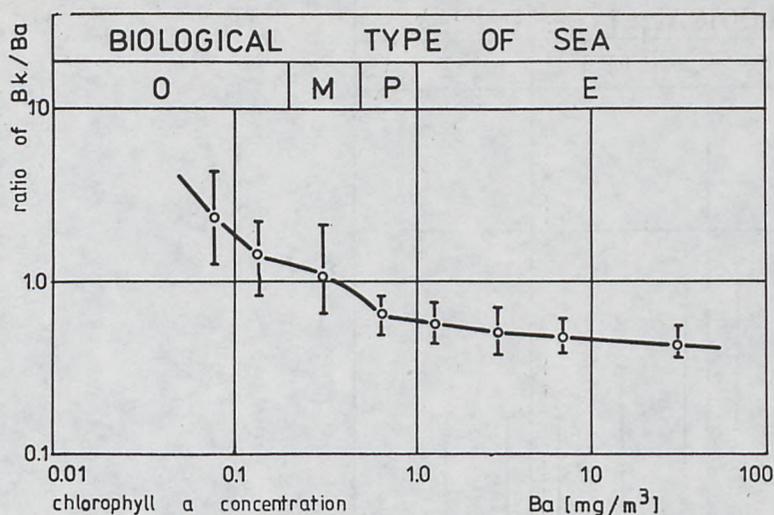


Figure 7: Bk/Ba ratio (carotenoids and chlorophyll a concentrations) changes depending on the biological type of phytoplankton. Vertical segments relate to standard deviations of the Bk/Ba ratios (Woźniak, in prepared)

production. Hence the domination of these pigments over chlorophyll is increased.

3.3. Pigments colour index as an indicator of the pigment composition in various phytoplankton

An often used indicator of the differentiation of the phytoplankton pigment composition is the so-called pigments colour index, C_{In} . It is defined as a ratio:

$$C_{In} = \frac{A_{433}}{A_{661}}, \quad (3)$$

of light extinction for wavelength $\lambda = 433\text{nm}$ — A_{433} , to light extinction for wavelength $\lambda = 661\text{nm}$ — A_{661} , measured in acetone phytoplankton extracts. In the first of these bands (433 nm) basically all the pigments (except phycobilins) absorb, in the band 661 nm however, mainly chlorophyll a absorbs. Hence the ratio of these extinctions is an "optical" measure of the ratio of the total pigments concentration to chlorophyll a .

Figure 8 presents the statistical dependences of the observed values of the colour index C_{In} on the chlorophyll a concentration, hence on the biological type of the sea. One can observe a significant decrease of C_{In} while changing from poorly productive seas to highly productive ones.

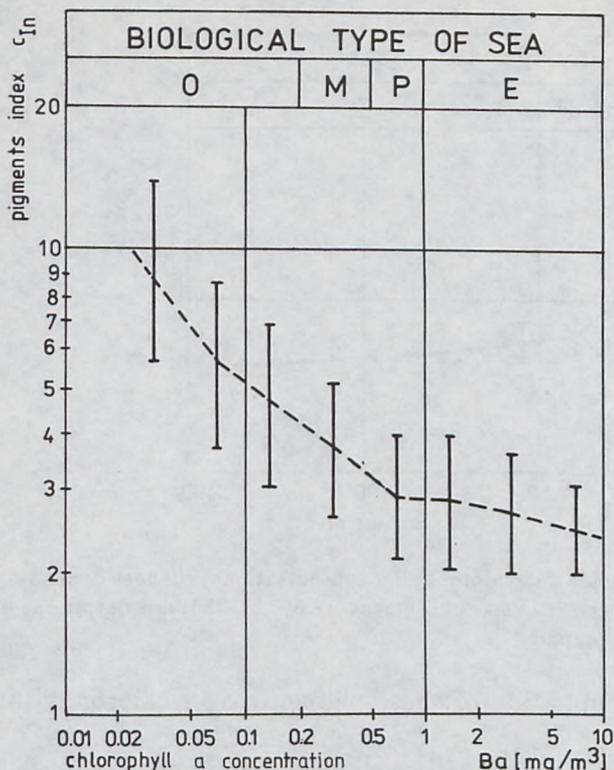


Figure 8: Statistical dependence of pigments colour index of sea phytoplankton C_{In} , on chlorophyll *a* concentration Ba . Vertical segments relate to standard deviations of the occurring magnitudes of the C_{In} index (Woźniak, in prepared)

This is due to significantly higher contributions of additional pigments in photosynthetic apparatus of oligotrophic phytoecenes, compared to phytoecenes in rich seas. It confirms the results presented in the previous paragraph.

3.4. Dependence of the composition and concentration of phytoplankton pigments on the depth in sea

Depth changes of the pigments composition and concentration cause the differentiation of the phytoplankton optical properties with depth. Experimental examples of such changes, observed in different World Ocean regions, shows Figure 9. Depth profiles of the pigments concentration using chlorophyll *a* Ba as an example are shown in Figure 9A. The depth changes of the colour index C_{In} presented in Figure 9B are the indication of the phytoplankton pigments composition changes with depth.

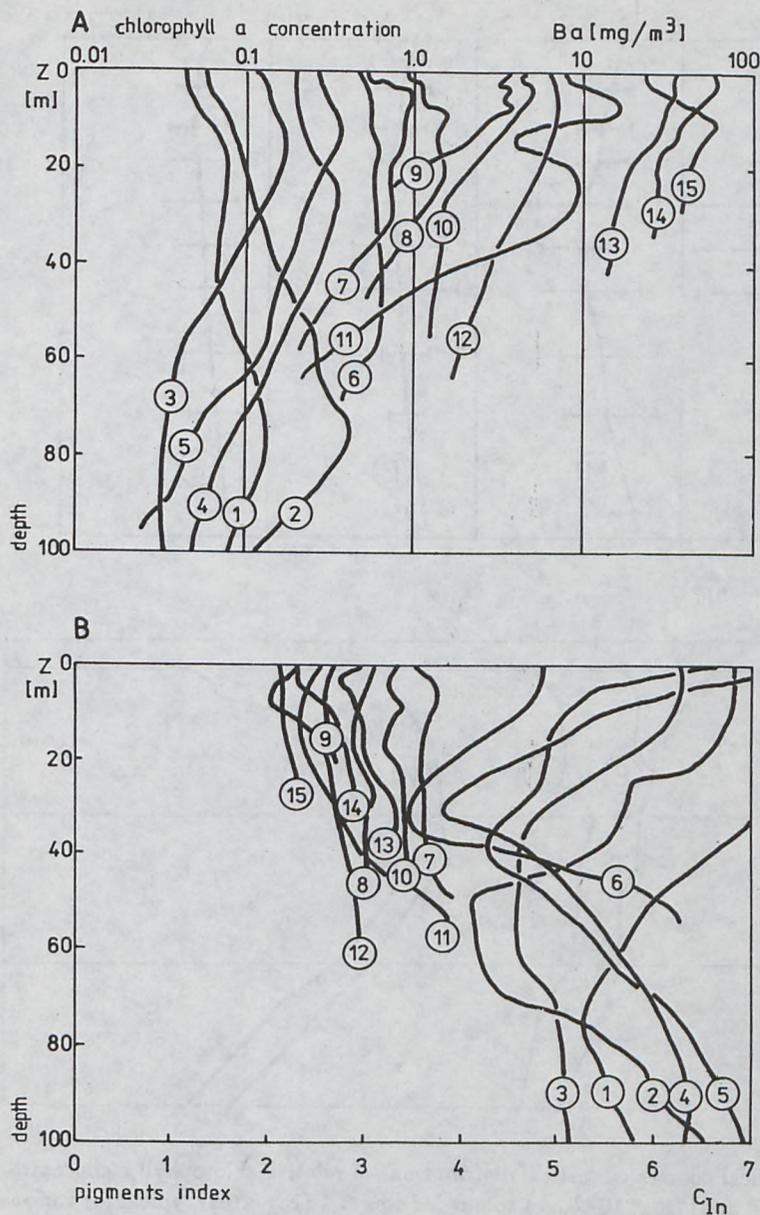


Figure 9: Experimental depth profiles: A - chlorophyll *a* concentration, B - pigments colour index C_{In} . 1 - Central Indian Ocean, 2 ÷ 5 - Central Atlantic, 6 ÷ 7 - Atlantic, Gulf of Ezcura, 8 ÷ 11, 13 - Baltic and Gulf of Gdańsk, 12, 14, 15 - Black Sea and Gulf of Burgas

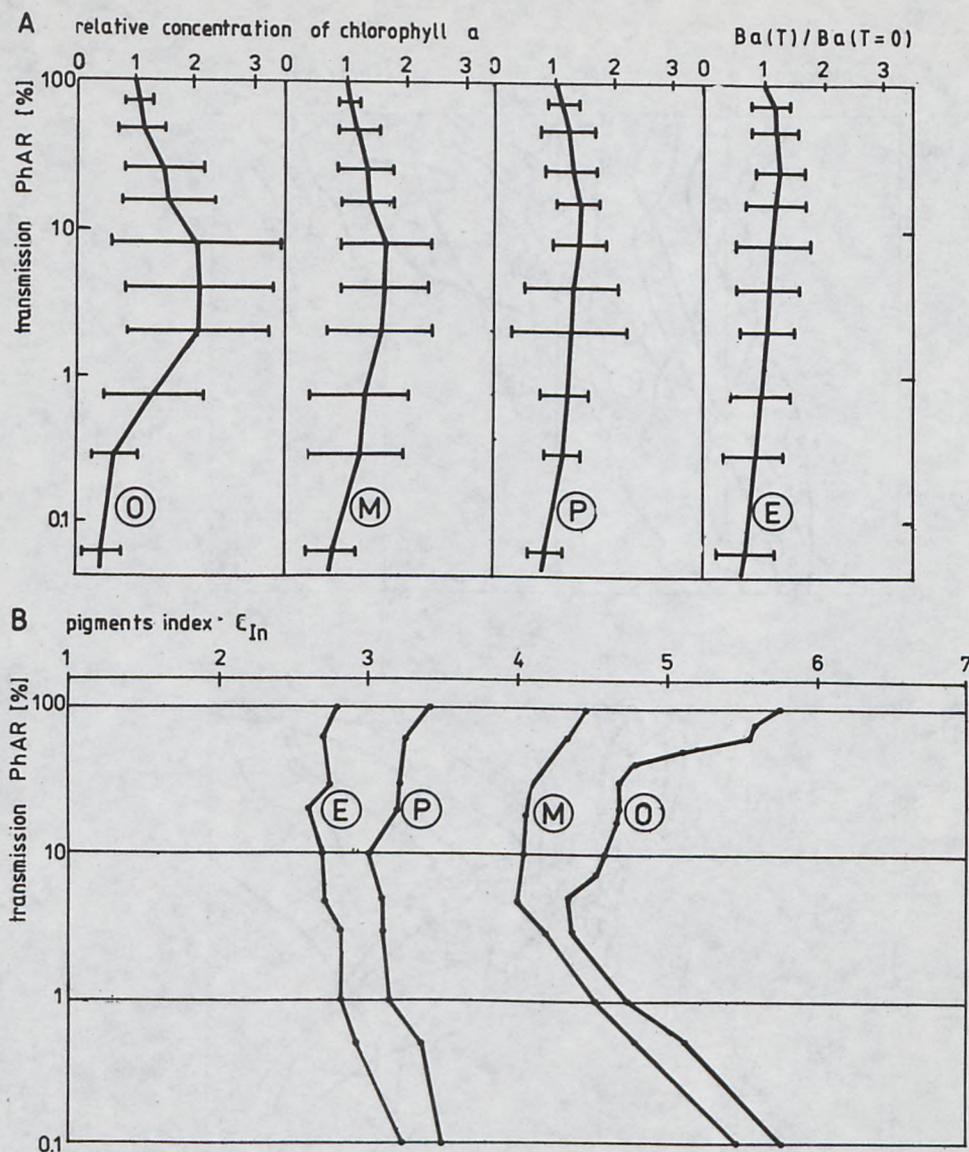


Figure 10: Statistical courses of vertical distributions of relative chlorophyll *a* concentrations $Ba(T)/Ba(T=0)$ (Fig. 10A) and colour indexes C_{In} (Fig. 10B) typical for various basins: O – oligotrophic seas [$Ba(0) < 0.2 \text{ mg/m}^3$]; M – mesotrophic seas [$0.2 < Ba(0) < 0.5 \text{ mg/m}^3$]; P – transient, meso-eutrophic seas [$0.5 < Ba(0) < 1.0 \text{ mg/m}^3$]; E – eutrophic seas [$Ba(0) > 1 \text{ mg/m}^3$]. Optical depth is expressed in the PhAR transmission scale into the depth. Horizontal segments in Figure 10A denote ranges of standard deviations of relative chlorophyll *a* concentrations (Woźniak, in prepared)

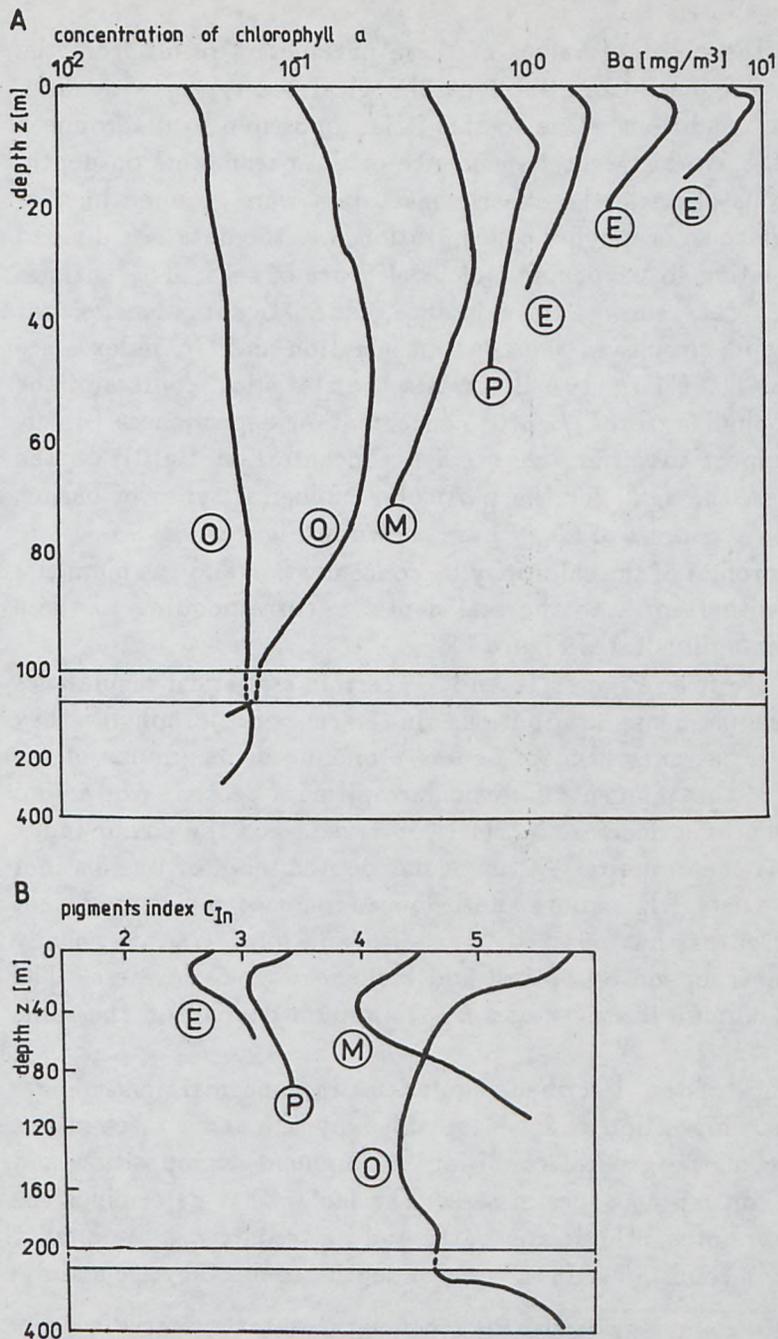


Figure 11: Exemplary hypothetical depth profiles for various biological types of seas: A - chlorophyll a concentration, B - pigments colour indexes (Woźniak, in prepared)

Differences in the absolute values of these parameters result from the fact that they originate from different biological sea types, with different vegetative conditions. Due to this it is impossible to determine a universal for the World Ocean dependence of the parameters on depth. To overcome this obstacle the experimental data were grouped in relation to the surface chlorophyll *a* concentration, *i.e.* the data was divided into groups relating to particular biological types of seas. The analysis of such grouped data, showed the existence of statistical tendencies that characterize depth profiles of the *Ba* concentration and C_{In} index – see Figures 10 and 11. Figure 10A illustrates the statistical courses of the relative chlorophyll *a* $Ba(T)/Ba(0)$ concentration dependences (determined with respect to surface chlorophyll concentration $Ba(0)$) on the optical depth in the sea⁶, for the particular biological types of basins. Similar statistical courses of $C_{In}(T)$ are shown in Figure 10B.

The depth profiles of the chlorophyll *a* concentration and the pigments colour index with respect to the real depth *z*, corresponding to these statistical courses, illustrates Figure 11.

As one can see from Figures 10 and 11, certain statistical regularities exist for vertical pigments distributions. In the case of chlorophyll *a* they consist in the occurrence of more or less pronounced maximums of the concentration of this pigment of particular optimum depths. Above and below these depths a decrease in *Ba* is observed. For the colour index the tendency is the opposite. At particular depths more or less distinct C_{In} minimum exists, while above and below an increase of this coefficient is observed. Depths that relate to max. *Ba* and min. C_{In} are usually similar and they depend on optical and biological type of waters. The chlorophyll maximum intensity and C_{In} minimum depend on the same factors⁷.

The existence of the described regularities in concentration changes and pigments composition can be explained by the same mechanisms as in the case of the general conditions of pigments composition and concentration for various types of seas. The factor that determines the phytoplankton photosynthetic apparatus and its resources is the quality of the vegetation conditions. In the case of depth profiles they are mainly:

⁶Optical depth in this paper is expressed in a scale of surface irradiance transmission into the sea. Its relation with real depth is $T = \frac{B(z)}{B(0)} = E(0) \exp \left[- \int_0^z K(z) dz \right]$, where: $E(z), E(0)$ – PhAR at a depth *z* and 0 m; $K(z)$ – vertical attenuation factor of the PhAR with depth in sea.

⁷A detailed analysis of the dependence of the location of an optimal for pigments zone in a sea and of the distinctness of the max. $Ba(z)$ and min. $C_{In}(z)$ on the optical and biological types of basins, is presented in Woźniak (in prepared) work

the irradiance level and the biogenic substances content. The irradiance decreases with depth, which causes a decrease in photosynthesis level and chlorophyll concentration at great depths. The light deficit causes there an increase in the additional pigments production rate, which is manifested by an increase in the pigments colour index.

The sea bottom is most often the source of nutrients, which means that their concentration increases with depth. The smallest it is in the surface layer, which limits the amount of phytoplankton (*i.e.* the chlorophyll *a* concentration). Similarly to light deficit at great depths, also the decrease of the biogens amount at smaller depths leads to additional production of accompanying pigments, hence an increase in the pigments colour index.

The net effect of the influence of the irradiance level and the biogenic substances content on phytoplankton resources is the appearance of a maximum in its concentration at intermediate optimum depths. At these depths the vegetation conditions are the best, therefore the contribution of the additional pigments in the photosynthetic apparatus is the least, which appears as a minimum at the depth profiles of C_{In} .

4. Final remarks

The analyses presented in this paper are limited to macroscopic, spatial distributions of phytoplankton in sea, neglecting their microstructure and such local phenomena as *e.g.* "Patchiness" (Bogucki, 1988). Except the seasonal changes, no time variations were analyzed (regular - like twenty-four hours changes, and also irregular). There is a lack of experimental material for statistical generalizations of these phenomena. On the other hand, selected aspects of time variability of pigments in sea and their spatial structures in different scales determined by means of fluorometric methods are described among others in Karabashev (1987) work.

The results of the generalized statistics presented in chapter 3, concerning the vertical distributions of pigments in a sea and their occurrence in various biological sea types, were utilized by the authors for phytoplankton absorption properties modelling in the sea. They can also be used as auxiliaries for the analysis of the total phytoplankton fluorescence properties. These problems are discussed more extensively in the next paper from this series (Woźniak and Ostrowska, 1990).

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